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Sound Production in Two Loricariid Catfishes

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SOUND PRODUCTION IN TWO LORICARIID CATFISHES

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SOUND PRODUCTION IN TWO LORICARIID CATFISHES

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SOUND PRODUCTION IN TWO LORICARIID CATFISHES

Amanda Lynn Webb August 2011 30 Pages

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Many families of catfish produce sounds via pectoral spine stridulation and/or swim bladder compression using sonic muscles attached to the swim bladder. The sound production capabilities and characteristics in Loricariidae, the largest catfish family, have not been well examined. Sounds produced by two loricariid catfish species, *Macrotocinclus affinis* and *Pterygoplichthys gibbiceps* were recorded. Both species produce broad band calls via pectoral spine stridulation. These species produce sounds by rubbing the ridges of the dorsal process of the pectoral spine base against the groove of the pectoral girdle. Call duration was generally shorter in *M. affinis* (2-15 ms) as opposed to those produced by *P. gibbiceps* (20-200 ms). Mean dominant frequencies were approximately 4000 Hz for *M. affinis* and 1000 (abduction) and 4500 Hz (adduction) for *P. gibbiceps*. Light and scanning electron microscopy were used to examine the dorsal process of the pectoral spines from the largest and smallest *M. affinis*, and from a wide range of sizes from *P. gibbiceps*. Mean distances between dorsal process ridges of *M. affinis* and *P. gibbiceps* were approximately 50 and 160 microns, respectively. For *P. gibbiceps*, dominant frequency was an inverse function of total length and inter-ridge distance.

CHAPTER 1

Background:

Sound is an integral part of both the terrestrial and aquatic environment. The difference in density in media through which sound travels affects sound propagation. Sound travels more effectively in liquid phases than in gaseous phases. In water, sound can travel up to five times faster than it would in air. In the deep ocean, 2,000 m and deeper, low frequency sounds (frequencies < 100 Hz) can be detected from distances thousands of miles away from the source. In more shallow waters, sounds are affected by many variables including water depth at a particular location, the type of bottom substrate, and roughness of the water surface to name a few (Bass & Clark, 2003). The uniqueness of the aquatic environment makes it an interesting area for investigating sounds produced by animals. Fish, similar to many other groups of animals, make sounds for a variety of reasons including spatial orientation (Tavolga, 1977), defense from predators, mating, alarm calls (Ladich & Fine, 2003), and as a response to stress (Ladich & Bass, 1998; Ladich, 2000).

The first written record of sound production in a fish dates back to the fourth century BC in Aristotle's *Historia Animalium* (Gohlke, 1957). Fish can produce sounds in several different manners including swim bladder compression, stridulation of the pectoral or dorsal spine, and grinding of teeth (reviewed in Ladich & Fine, 2003). Some fishes, including several catfish taxa, can produce sound through multiple mechanisms.

Of the approximately 28,000 extant species of fish, Siluriformes (the catfishes) is a very species rich order, with approximately 2,700 species (Teugels, 2003). Geoffrey Saint-Hilaire recorded the first description of sound production in catfish in 1829

(Ladich, 2003). Some species of catfish produce sounds through pectoral spine stridulation or through swim bladder compression using sonic muscles. Some catfish species are able to produce sounds through both mechanisms (Ladich & Fine, 2006). In addition to producing sounds, catfish are also known to use their pectoral spines for predator avoidance and defense. When the spine is completely abducted and locked, it makes the fish harder to be eaten and the pointed tip of the spine serves as an anti-predator weapon (Fine & Ladich, 2003).

Sound production in teleosts (bony fishes) via swim bladder compression has been well studied (Demski et al., 1973). The swim bladder is quickly contracted and extended by the sonic muscles, which causes its radiating surface to vibrate. There are two types of sonic muscles. Both ends of intrinsic muscles are directly attached on to the swim bladder whereas extrinsic muscles have one insertion point on another nearby structure. Extrinsic muscles may be attached to bones such as the skull or the vertebrae (Ladich & Fine, 2003). It has been suggested that swim bladders aid in propagating sounds generated from other structures in the body (Demski et al., 1973). However, when the swim bladders were deflated in channel catfish, which produce sounds via pectoral spine stridulation, no significant difference in the amplitude or power spectrum was observed (Fine et al., 1997). Further studies are needed to examine the relationship between swim bladder and stridulation sound production as the sample size was relatively small in the Fine et al. study and one species may not be representative of all catfish. Some catfishes, such as those in the family Doradidae, are known to be able to modulate the frequency of their sound, most likely by changing the speed at which the fish contracts its sonic muscles (Ladich, 1997).

Contrary to swim bladder sound production, stridulatory sounds are made when fish rub together spines or bones. These sounds have been described using numerous terms including clicks, squeaks, chirps, croaks, and grunts (Kaatz, 1999; Heyd & Pfeiffer, 2000). The vast majority of sounds produced by spine stridulation are made using the pectoral spine. Many catfish taxa, including Loricariidae produce sounds through the abduction and/or adduction motion of the pectoral spine striking against the pectoral girdle. The dorsal process, on the topside of the pectoral spine sits in the medial groove of the cleithrum (Fine & Ladich, 2003). The ventrolateral surface of the dorsal process of the pectoral spine contains ridges which are depressed against a slightly concave, rough, and featureless fossa floor in loricariids (Schachner, 1977; Fine, et al., 1997). Fine and Ladich (2003) suggested that each ridge scraped across the cleithrum creates a single pulse. Some species of catfish, including some in the families Ictaluiridae, Pimelodidae, and Loricariidae, have ridges on the dorsal spine as well (Schachner, 1977; Fine et al., 1997). Sound production via dorsal spine stridulation has not been well described.

Stridulatory sounds are frequently made as disturbance calls. Often this occurs when the fish is held under water or in the air (Kaatz, 1999), which is a common method of eliciting sounds from catfish for recordings. It has been noted that catfish are apt to stridulate more when held in the air (Ladich, 1997; Heyd & Pfeiffer, 2000). Sörensen (1895) suggested that stridulatory disturbance sounds may function in defense against predators by calling attention to the sharp end of the spines. However it was observed that stridulatory sounds did not deter a piranha from eating a doradid catfish (Markl, 1968).

This thesis describes the stridulatory sounds of two catfishes in the family Loricariidae, *Macrotocinclus affinis* and *Pterygoplichthys gibbiceps*. Chapter 2 describes the bioacoustics of this sound production in terms of characteristics of the sounds and the anatomy of the structures used to produce the sounds. Chapter 3 is a summary of the findings of this study and describes potential future research directions.

CHAPTER 2

Introduction:

Loricariidae is the largest family in the order Siluriformes, suborder Loricarioidei, and contains over 600 species, almost one-third of all living catfishes identified (Briggs, 2005). This family, known as the armored suckermouth catfishes, possess several unique morphological characteristics including a bi-lobed swim bladder and fenestrae in the skull that are hypothesized to posses acoustical functionality (Weitzmann, 2005). The swim bladder is located in the bony capsule-like structures on both sides of the ear structures posterior to the eyes. The fenestrae are lateral to the swim bladder and dorsal to the pectoral spine in the large complex bone called the pterotic+supracleithrum (Weitzmann, 2005). It is not yet known if the proximity of the pectoral spine to the swim bladder has any effect on sound production via pectoral spine stridulation. Although approximately 90 loricariid species have been examined for sound production capabilities, fewer than 10 species (*Ancistrus sp., Hypostomus sp., Otocinclus sp., Panaque maccus, Peckoltia pulcher, Planiloricaia cryptodon, Rhineloricaria sp.,* and *Sturisoma aureum*) have been observed or recorded during disturbance calls when handled. The base of the pectoral spine was only studied microscopically in six of the above species, including only one specimen from the genus *Otocinclus* (now known as *Macrotocinclus*; Kaatz et al., 2010).

The first loricariid catfish chosen for this study was *Pterygoplichthys gibbiceps*, also known as the leopard or sailfin plecostomus and grows to approximately 50 cm. *P. gibbiceps* was originally described by Kner (1854). This species is found in the middle to upper sections of the Orinoco and Amazon rivers that run through Brazil, Peru, and

Venezuela. The second loricariid chosen for the study was M*acrotocinclus affinis*, also known as the golden or dwarf oto. Catfishes in this genus are found in small, quiet margins of large rivers in the tropical lowlands of South America. *M. affinis* was originally discovered by Steindachner in 1877 (Hans & Ingo, 2005) in Rio de Janiero, Brazil. They prefer environments with clear freshwater, modest water flow, high oxygen levels, and broad-leaf grasses. Species in this group, including *M. affinis*, grow to approximately 45 mm SL (Schaefer, 1997; Hans & Ingo, 2005). Both species use their mouth as a sucker to attach themselves to substrates and to feed on algae.

Ladich (1997) and Heyd and Pfeiffer (2000) stated that loricariids only stridulate during the abduction of the pectoral spine unlike bagrids, mochokids, doradids, and aspredinids which stridulate during both adduction and abduction. To the contrary, Kaatz (1999) noted sound production in abduction-adduction pairs are most common in loricariids. This suggests that some variation in sound production patterns may be possible in this taxon. Species within the loricariid family may have a characteristic sound production pattern, but the taxa within that family are not necessarily restricted to that one pattern. Preferences may also exist between individuals for either their right or left side, and sounds may be produced primarily by one fin or alternating between the two (Fine et al., 1995).

The objective of this study was to test two loricariid catfishes that vary considerably in size, *P. gibbiceps* and *M. affinis*, for their sound production capabilities and to quantify acoustic characteristics of the sounds they produce. The bone structures and mechanisms used in sound production, as well as the relationship between stridulatory structures and the sounds produced were also examined.

Materials and methods:

Experimental Animals

The species examined were *Pterygoplichthys gibbiceps* (Figure 1A) and *Macrotocinclus affinis* (Figure 1B). Both species are commonly found in the aquarium trade. *P. gibbiceps* is commonly known as the leopard plecostomus and reaches a maximum total length of approximately 50 cm. *M. affinis* is known as the midget or dwarf suckermouth catfish and only grows to approximately 4 cm in total length. The fish were fed an algae pellet diet, maintained in 38 to 150-L aquaria, and kept on a 12-hour light/12-hour dark cycle. Twenty-two *P. gibbiceps* and ten *M. affinis* were used in this study.

Sound Analysis

Three sets of audio recordings were taken from each fish. Each individual was held approximately 3 cm below the surface of the water in a 19-L container and approximately 3 cm away from a GRAS type 10CT hydrophone (calibration sensitivity of -195 dB re 1 V/µPa; ± 3 dB, 0.02-10 kHz, omnidirectional, Denmark). The hydrophone was connected to a Kistler charge amplifier type 5010, which was attached to a desktop computer. All the fish were held by the left pectoral spine using a common procedure to elicit sounds. Holding a fish by one pectoral spine while the other spine produces sounds is a common method of recording sound production in catfishes (as reviewed in Kaatz 1999). Each recording session lasted approximately two minutes with two minutes of rest in between recordings. Raven 1.2.1. sound recording and analysis software (sample rate 44.1 Hz, FFT: 512 samples, Hann 50% overlap, 3 dB filter

bandwidth= 124 Hz, 16-bit signed PCM, saved as .wav files) was used to record and measure call duration for each audio file. SoundRuler 0.9.6.0 sound analysis software was used to measure dominant frequencies in each audio file. Dominant frequency is defined as the frequency with the most energy. Sound analysis was performed on the five most clear and distinct calls from each *P. gibbiceps* and on the five most intense single adduction clicks from each *M. affinis*. Sounds were analyzed in respect to pulse type (abduction or adduction), dominant frequency, and duration of pulse sets and clicks.

Morphological analysis

Morphological studies were performed on the left pectoral spine from the largest and smallest *M. affinis*. As a representative subset of the range in size, left spines of fourteen of the twenty-two *P. gibbiceps* were examined. The specimens were dissected, cleaned using either a dilute soap solution in an ultrasonic jewelry cleaner or by a dermestid beetle colony. Images of the left spine and cleithrum from a representative *P. gibbiceps* were taken using light microscopy to examine the position of the spine in the pectoral girdle. The samples to be studied using scanning electron microscopy (SEM) were mounted on SEM stubs and gold-palladium sputter coated using an Emscope SC500 vacuum evaporator. SEM micrographs were captured using a Jeol JSM-5400LV scanning electron microscope and IXRF Systems Inc. 500 Digital Processing system and software.

The dorsal processes of the pectoral spines are covered with parallel ridges. The inter-ridge distances, the spaces between the crests of two ridges, were measured using Auto-Montage Pro 5.02 beta software (Syntopics Ltd). Auto-Montage measures

distances in three dimensions when calibrated with a Leica MZ16 light microscope. A series of Z-stacks images taken every 10-20 microns was used to accurately measure the inter-ridge distances. Modeling dough was used to place and hold the pectoral spines so that the spines on the dorsal process were parallel to the surface of the table and facing up. Using the motorized focus knob, the microscope was focused on the ridge farthest from the microscope. This position was set as the first Z-stack in the Montage software. The microscope was then focused on the ridge closest to the microscope and this position was designated as the last Z-stack. The number of Z-stacks was chosen experimentally to produce the clearest picture and varied between 15 and 25, depending upon spine size. After each Z-stack was captured, the software identified the in-focus portions of each Z-stack to create a single image collage where most of the ridges were in focus. To measure the distance between ridges, markers were manually placed in the center of each ridge on the compiled Montage image. The software used the known distances between the Z-stacks in addition to the distances in the x and y coordinates to accurately calculate inter-ridge distances.

Statistical analysis

Analysis of variance (ANOVA) was used to test for relationships between dominant frequency and the following: species, call types in *P. gibbiceps*, and total length in *P. gibbiceps*. ANOVA was also used to test for differences in pulse duration between species, between call types in *P. gibbiceps*, and for differences in inter-ridge distances between the two species and between sizes. Where appropriate, the Shaprio-Wilk test was used to check the data for normality. The relationship between inter-ridge distance

and dominant frequency of Type A pulses in *P. gibbiceps* was examined using linear regression analysis.

Results:

Sound production

Both species produced sounds through pectoral stridulation that were broadband in frequency. *P. gibbiceps* generally produced sounds in pulse trains through a pattern of abduction and adduction of the pectoral spines (Figure 2A-B). Type A calls or "low-squeaks" were produced by abduction and Type B pulses or "high-squeaks" were produced by adduction of the pectoral spine with Type A calls having lower dominant frequencies than Type B calls. Pulse trains generally consisted of several sets of abduction (low) and adduction (high) "squeaks". Occasionally a series of Type A only pulses were also recorded. *M. affinis* produced single "clicks" by adduction only.

The dominant frequency for *P. gibbiceps* Type A pulses (Table 1) ranged from 200 to 1200 Hz with a mean (± SE) value of 1019 (± 184) Hz and Type B pulses ranged from 350 to 10000 Hz with a mean (± SE) value of 4522 (± 1263) Hz. The dominant frequency for clicks produced by *M. affinis* ranged from 1200 to 6600 Hz with a mean (± SE) value of 4049 (± 557) Hz (Table 1). The mean dominant frequency differed significantly ($P < 0.01$) between the two species and between the two pulse types from *P. gibbiceps* ($P < 0.01$).

Mean (± SE) call duration for *P. gibbiceps* Type A pulses were 193 (± 19) ms compared to Type B pulses which were 84 (± 5) ms (Table 1). Clicks from *M. affinis* ranged in duration from 2 to 34 ms with a mean (± SE) duration of 13 (± 5) ms. Type A

pulses were significantly longer in duration from pulse Type B ($P < 0.01$) and from *M. affinis* clicks ($P < 0.01$), but pulse Type B "high-squeaks" did not differ significantly in duration from the *M. affinis* "clicks" ($P > 0.05$; Table 1).

Morphology

The pectoral spines of both species articulate inside the pectoral girdle (Figure 3A), which is composed of several fused bones, the largest of which is the cleithrum (Figure 3B). The pectoral spine rests in the spinal fossa of the cleithrum. The points of articulation are similar to those in the channel catfish as described by Fine et al. (1997). The pectoral spines of both species have three processes: dorsal, ventral, and anterior (Figure 4). The dorsal process is the largest of the three and has ridges in its ventrolateral surface. During stridulation, the ridges on the spine are struck against the spinal fossa of the cleithrum. Both species were capable of locking their spines when fully abducted.

The mean (± SE) inter-ridge distance found on the dorsal process of left pectoral spines was 162 (± 23) microns for *P. gibbiceps* (Figure 5A), and 53 (± 1) microns for *M. affinis* (Figure 5B). The inter-ridge distances were significantly different between species ($P < 0.01$). There was also a significant difference in inter-ridge distances between the smallest (5.1 cm TL) and largest (22.5 cm TL) *P. gibbiceps* ($P < 0.01$), but not between the smallest (3.4 cm TL) and largest (4.1 cm TL) *M. affinis* ($P > 0.05$; Figure 6). There was a significant linear regression relationship between total length and inter-ridge distance in *P. gibbiceps* ($P < 0.0001$; Figure 7).

In examining the relationship between dominant frequency and total length, only the data from *P. gibbiceps* was used because of the limited range in total length in *M.*

affinis. The mean dominant frequency for each of the twenty-two *P. gibbiceps* used was obtained from only Type A pulses since not all individuals produced Type B pulses. There was a significant linear regression relationship between total length and dominant frequency and between inter-ridge distance and dominant frequency ($P < 0.001$). As total length and inter-ridge distance increased, mean dominant frequency decreased (Figure 8).

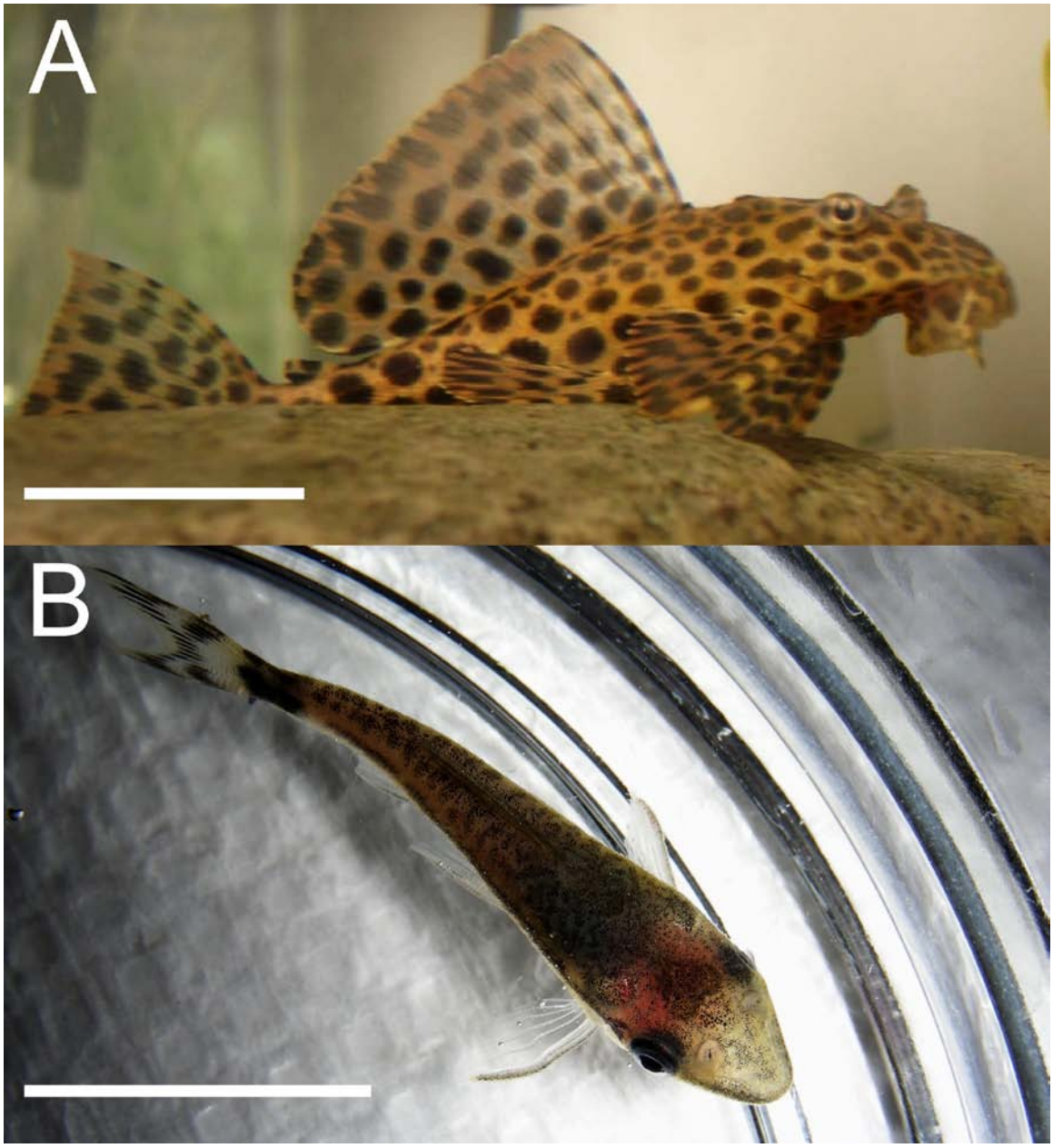

Figure 1: A) *Pterygoplichthys gibbiceps* B) and *Macrotocinclus affinis*. Scale bars for A and B = 2 and 1 cm, respectively.

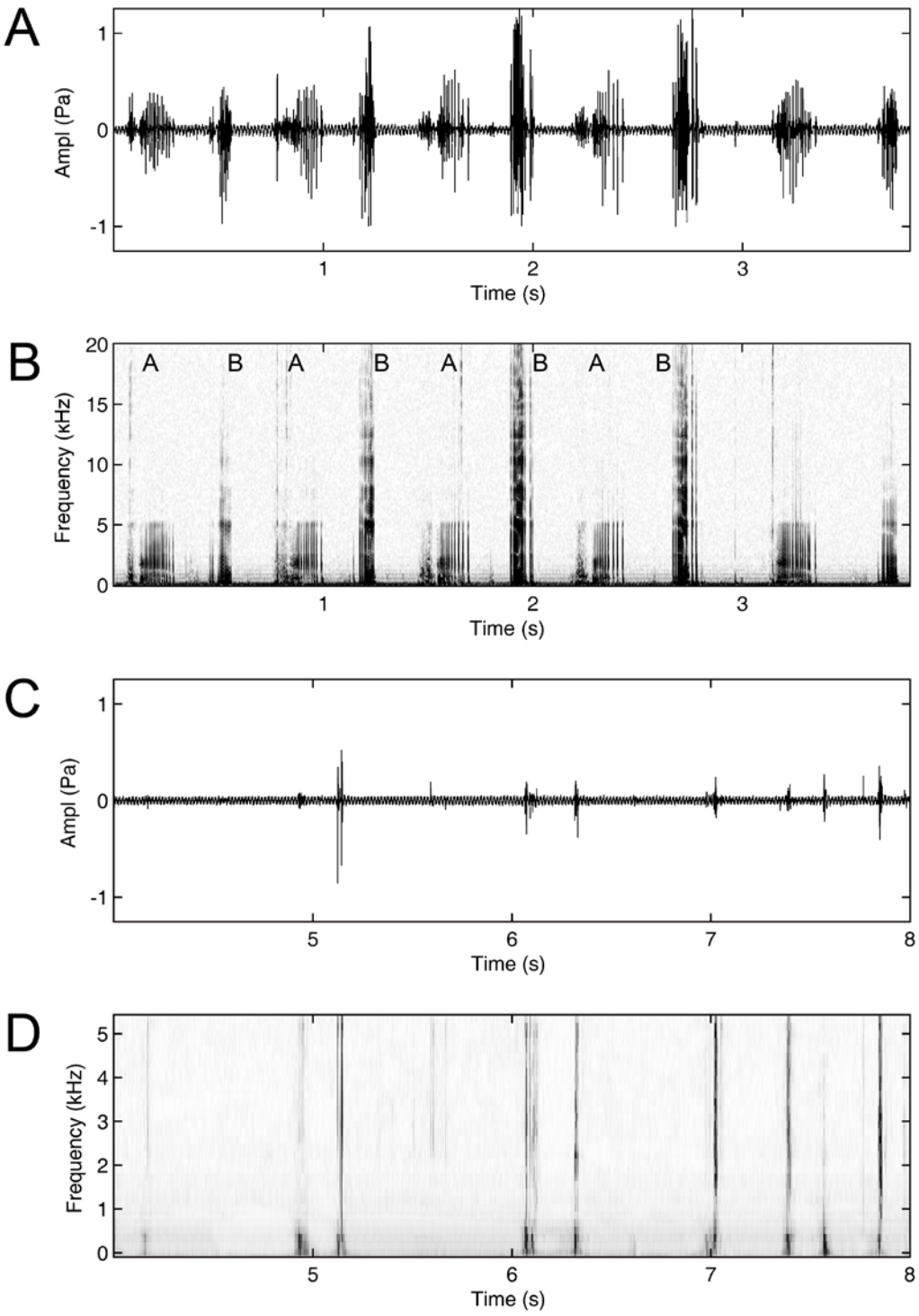

Figure 2: A) Oscillogram and B) spectrogram of *P. gibbiceps* stridulatory sounds. The lower frequency Type A calls are produced through pectoral spine abduction, the higher frequency Type B calls through adduction. C) Oscillogram and D) spectrogram of *M. affinis* stridulatory sounds. Single "clicks" were produced through pectoral spine adduction.

Table 1: Mean and standard error for total length, dominant frequency, and pulse duration for the two studied species. *P. gibbiceps* pulses were divided into abduction (Type A) and adduction (Type B).

Species	N	Length Range (cm)	Mean Total Length (cm)	Dominant Frequency (Hz)	Pulse Duration (ms)
O. affinis	10	3.5 - 4.1	3.75 (± 0.07)	4049 (± 557)	13 (± 3)
P. gibbiceps Type A	7	6.1 - 15	9.74 (± 0.4)	1019 (± 184)	193 (± 19)
P. gibbiceps Type B	6	8.6 - 15	9.88 (± 0.5)	4522 (± 1263)	84 (± 5)

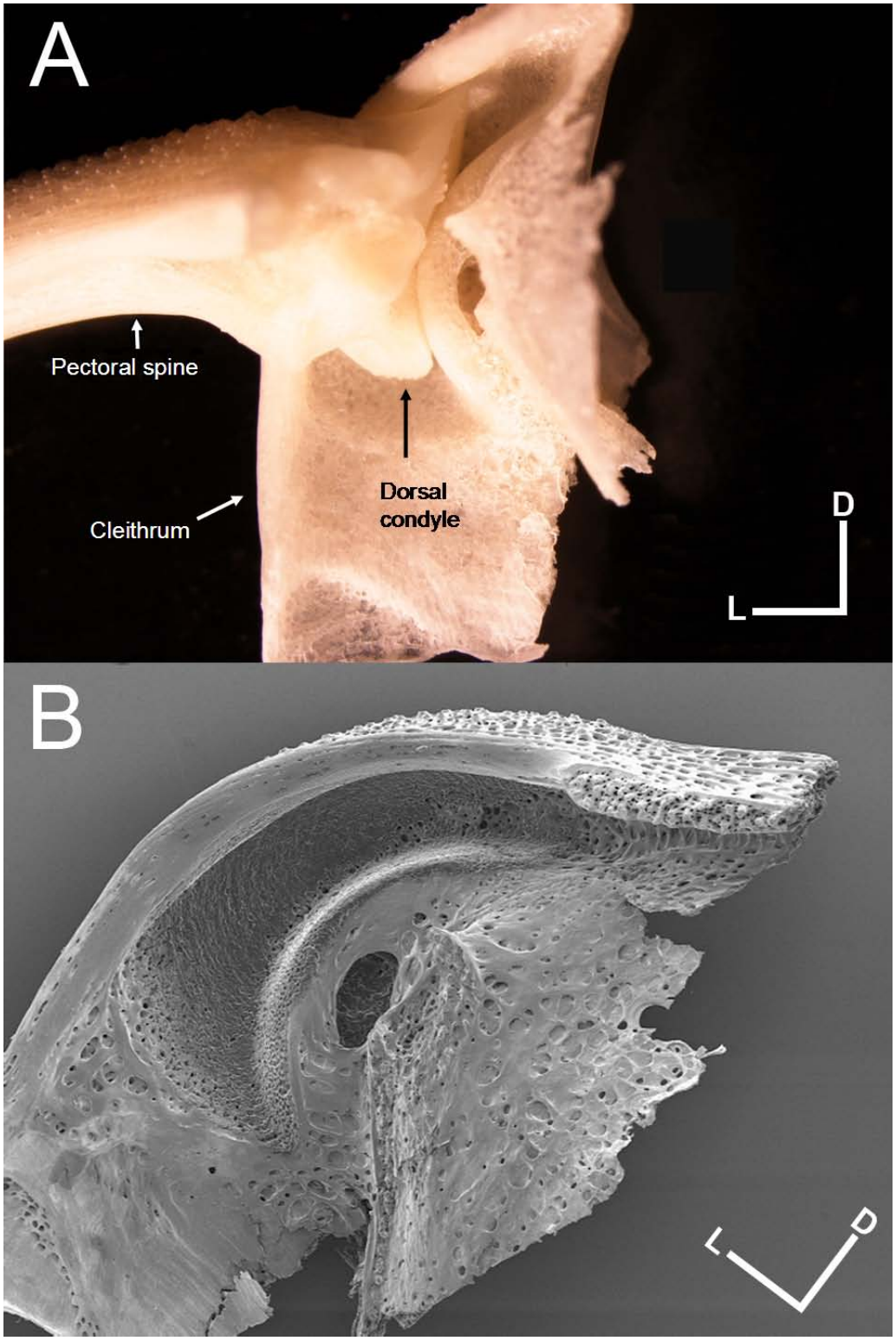

Figure 3: A) Light and B) scanning electron micrographs of the ventral view of the right cleithrum of a *P. gibbiceps*. While A) shows the pectoral sine in place in the cleithrum, the spine has been removed in B) to expose the dorsal fossa of the cleithrum. D = dorsal, L = lateral.

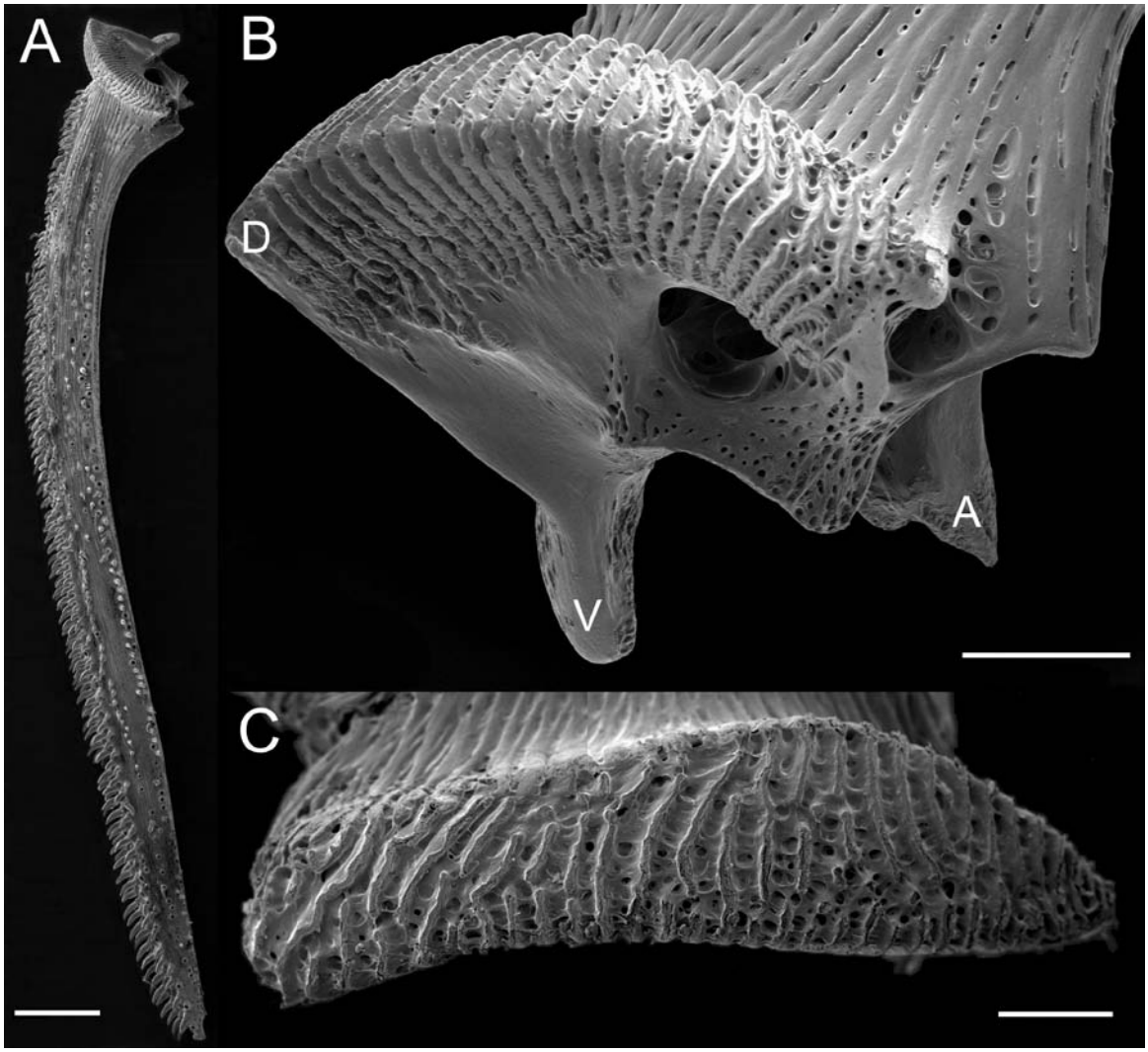

Figure 4: Scanning electron micrographs of a left pectoral spine of *P. gibbiceps* (TL = 11.9 cm, mass = 12.5 g). A) Dorsal view of complete spine. B) Base of pectoral spine and its processes: ventral (V), anterior (A), and the dorsal process (D) of *P. gibbiceps*, showing ridges. C) Dorsolateral surface of the dorsal process of *M. affinis* (TL = 4.1 cm, mass = 0.68 g). Scale bars = A) 3 mm B) 2 mm C) 0.5 mm.

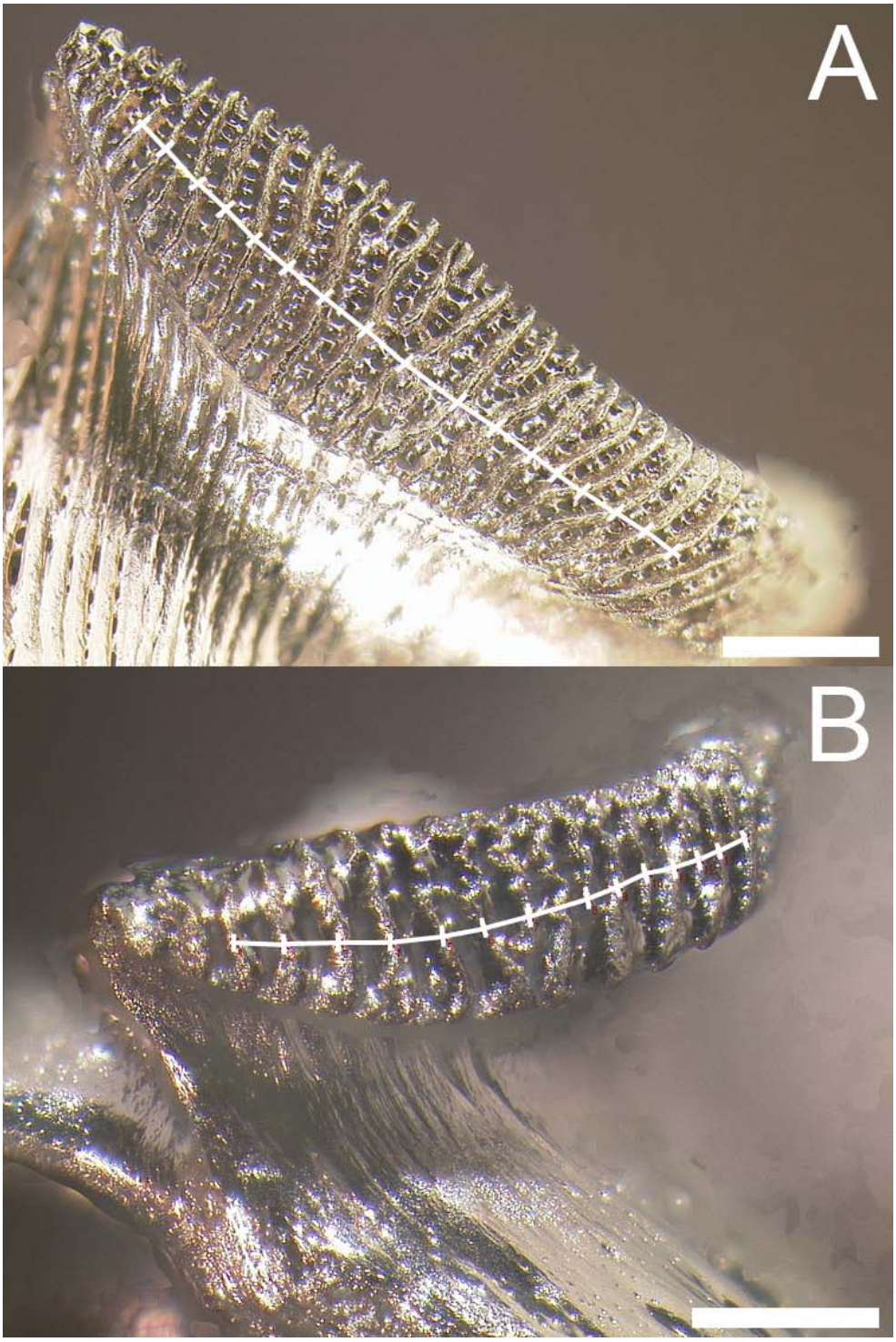

Figure 5: Sample light microscopy images of the proximal end of gold-palladium-coated left pectoral spines of A) *P. gibbiceps* and B) *M. affinis*. Images were produced by merging multiple, in-focus Z-stack photographs and were used to measure three dimensional inter-ridge distances. Hash marks represent the distance from one ridge to another. Scale bars = A) 0.5 mm B) 0.2 mm.

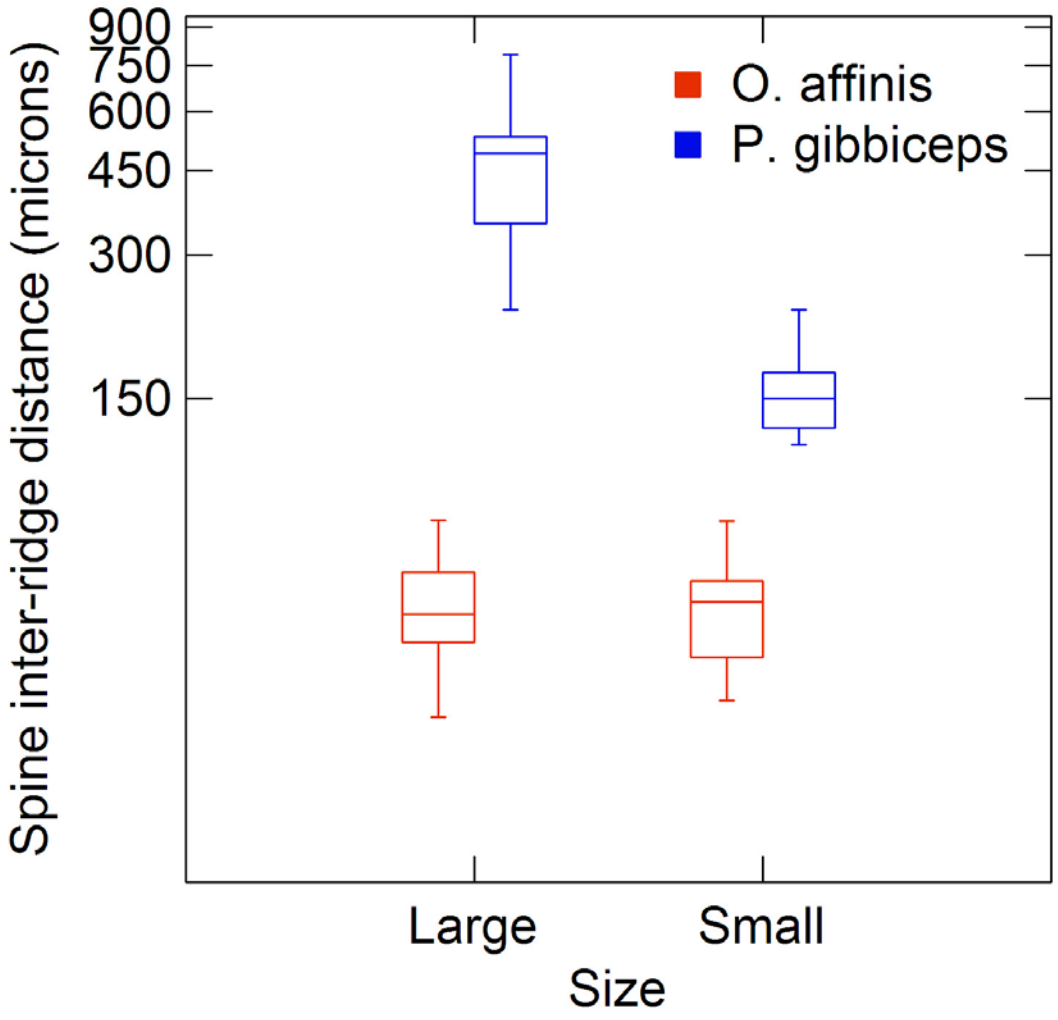

Figure 6: Pectoral spine inter-ridge distance as a function of species and size. Box plots of inter-ridge distances for individual fish (the smallest and largest representative for *M. affinis* and *P. gibbiceps*). Box plots display the median, 25th and 75th percentiles (box), and the 10th and 90th percentiles (whiskers).

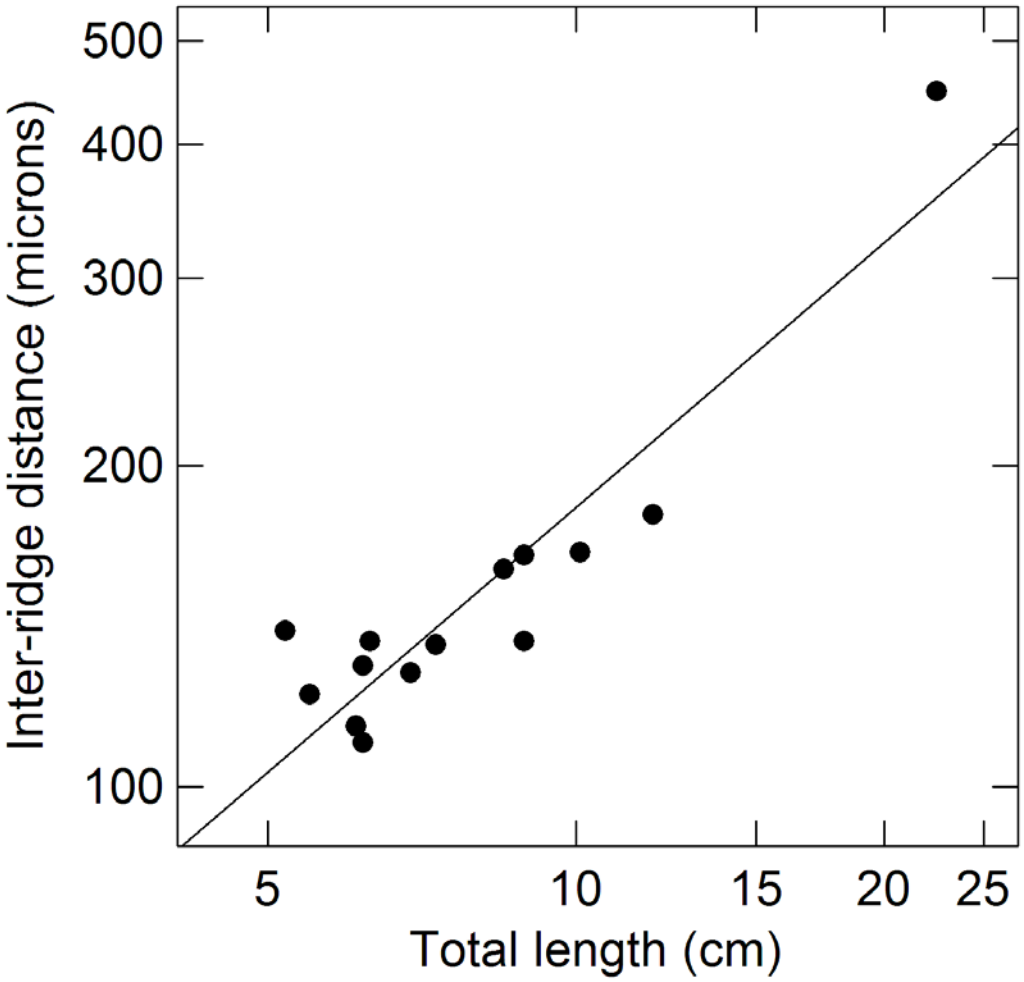

Figure 7: Relationship in *P. gibbiceps* between inter-ridge distance and total length. A significant linear regression relationship is exhibited (Distance = 18.5 (TL) + 3.4; R^2 = 0.93, $P < 0.0001$).

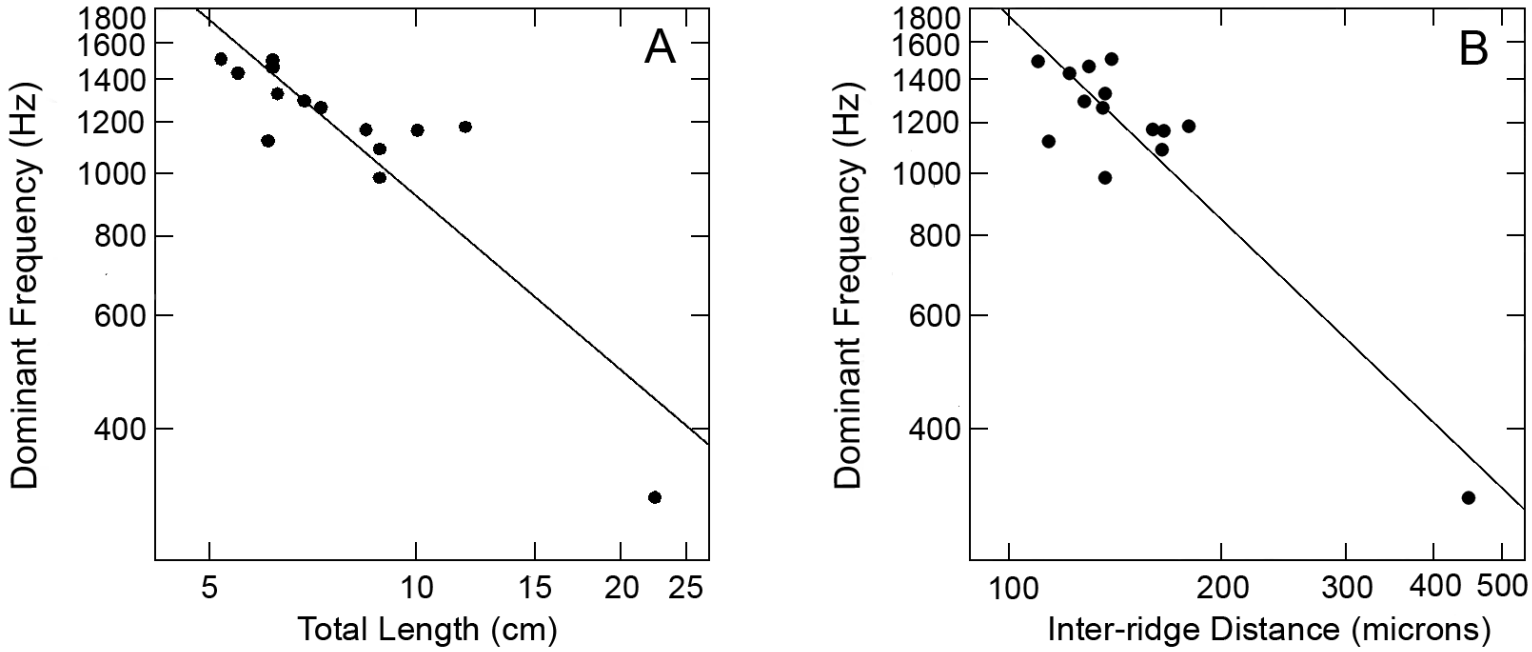

Figure 8: Relationship in *P. gibbiceps* between dominant frequency and A) total length and B) pectoral spine inter-ridge distance. The trend lines represent power functions with the following equations: A) $y = -65.52x + 17{,}368$, $R^2 = 0.84$; B) $y = -3.128x + 1706.8$, $R^2 = 0.78$.

Discussion:

Both *M. affinis* and *P. gibbiceps* are capable of producing broadband sounds as have been found in other families of catfishes including Pimelodidae, Mochikidae, Doradidae (Fine et al., 1997) and Callichthyidae (Pruzsinszky and Ladich, 1998). As in other catfish, such as the channel catfish *Ictalurus puctatus* (Fine et al., 1995), sounds were produced exclusively through pectoral spine stridulation, especially when disturbed or distressed. This is similar to sound production in the armored catfish *Corydoras paleatus* (Pruzsinszky and Ladich, 1998) and the Mochokids (Paramentier et al., 2010). The findings in the current study are in agreement with the modified and compiled topology presented in Kaatz et al. (2010). In the Kaatz topology, the family Loricariidae was represented by eight species (*Ancistrus* sp., *Hypostomus* sp., *Otocinclus* sp., *Panaque maccus, Peckolita pulcher, Planiloricaria cryptodon*, *Rhineloricaria* sp., and *Sturisoma aureum*) and were observed to be vocal (i.e., sound-producing) when handled, as were *P. gibbiceps* and *M. affinis* in the current study. The families Loricariidae and Callichthyidae are the only families in the suborder Loricarioidei that are known to be vocal. The other families (Nematogenyiidae, Trichomycteridae, Scoloplacidae, and Astroblepidae) are silent. That is, no disturbance sounds have been recorded or observed when they are handled (Kaatz et al. 2010).

In the current study, the pulse patterns differ between the two species. *P. gibbiceps* generally produced sounds by alternating between abduction and adduction, while *M. affinis* produced sounds only through adduction. This adduction only pattern of *M. affinis* is opposite of that seen in Pimelodidae (Ladich 1997), the callichthyid catfish *Corydoras paleatus* (Pruzsinszky and Ladich, 1998), *Bunocephalus* species (Gainer,

1967) and many ictalurid catfishes (Fine et al., 1995; Fine et al., 1997). As is common in catfish from the families Pimelodidae, Doridiidae (Ladich, 1997) and Mochokidae (Ladich, 1997; Paramentier et al., 2010), *P. gibbiceps* produced sounds through abduction-adduction pairs. However, unlike Pimelodidae, *M. affinis* and *P. gibbiceps* did not produce sounds through both pectoral spine stridulation and swim bladder compression (Ladich, 1997). It is not surprising that loricariids do not produce sounds with their swim bladders since their swim bladders are greatly reduced and encased in a bony capsule close to the ears.

Similar to other studies, the dominant frequency of sounds produced tended to decrease with increasing fish size, both within *P. gibbiceps* and between *M. affinis* and *P. gibbiceps*, which vary considerably in size. Paramentier et al. (2006) noted that the size of two species of pearlfish (Carapidae) was negatively related with frequency. Similar relationships have also been noted in auchenipterids, doradids (Kaatz, 1995), damselfish (Myrberg et al., 1993), and weakfish (Connaughton et al., 2000). The frequency range for *P. gibbiceps* Type A pulses is similar to that of catfish from the superfamily Ariodei, which exhibit the most energy in stridulatory sounds between 1,000 and 4,000 Hz (Kaatz, 1999), while *P. gibbiceps* Type B pulses and *M. affinis* clicks fell slightly above the 4,000 Hz mark.

As noted by Fine et al. (1999) and also seen in the current study, as fish grow in total size, their pectoral spine inter-ridge distances also increase. The relationship between inter-ridge distances on pectoral spines and sound production in catfishes had not been previously examined. This relationship would likely be stronger if not for the natural variance in sound production by individual fish of the same species. High levels

of variance in frequency of sound production have also been reported in mochokid catfish (Paramentier et al., 2010) and in *Ictalurus punctatus* (Fine et al., 1997). The variability in dominant frequency in sounds produced by *P. gibbiceps* may be due in part to the variability in call duration within individuals. Fine et al. (1999) noted that some variation is likely due to modulation of speed, spine ridge depression, call patterning, and number of fin sweeps.

During observation of the fish in laboratory aquaria, no spontaneous sounds were recorded from single *P. gibbiceps*. In laboratory aquaria with gravel, plants, and large rocks to hide under, groups of *M. affinis* did produce sounds spontaneously in addition to sounds produced as a stress invoked response (personal observation). It is not known yet if the sounds elicited by distress differ significantly from spontaneously emitted sounds in these two species.

CHAPTER 3

Summary and Future Directions:

In summary, the two loricariid catfishes, *P. gibbiceps* and *M. affinis*, produce sounds through pectoral spine stridulation, similarly to other catfish species. These sounds are produced when the ridges on the dorsolateral surface of the dorsal process of the base of the pectoral spine are rubbed against the pectoral girdle. *P. gibbiceps* sounds were produced through alternating abduction and adduction of the pectoral spine and were longer in duration and lower in frequency than sounds from *M. affinis* which were produced only through adduction. As pectoral spine inter-ridge distance and total length increased, dominant frequency decreased.

Just as humans exhibit handedness, some catfish, such as the channel catfish may show a preference for either their left or their right pectoral spine when being used for sound production. Although sounds can be produced from either side, an individual may choose to primarily use one over the other (Fine et al., 1999). The two species in the current study have not yet been examined for a preference as all fish were restrained by the left pectoral spine. If these two species do have a preference, it would be interesting if there are any differences in wear patterns on the ridges of the dorsal process of the pectoral spine on the left and right spines.

As of yet, it is not known if there is a significant difference between sounds produced by distress or spontaneously emitted sounds, or between sounds recorded in the wild versus those in captivity in either of these two species. The functional significance of their sounds in the wild is also largely unknown although some biologists have

questioned if the sounds served any purpose at all, as mentioned by Fine and Ladich (2003). Kaatz (1999) suggested that stridulation evolved as a means of defense against predators and notes that this method of sound production is more often used in disturbance calls. For example, doradids (*Platydoras castatus*) and pimelodines (*Pimelodus blochii*) (Ladich, 1997) produce sounds through stridulation rather than through drumming when held in air, although they can produce both types of sounds. There is some evidence for the purpose of catfish sound production. Although the sea catfish (*Arius felis*) produces sounds using its swim bladder, it uses those sounds for detecting objects (echolocation) and for directionality (Tavolga, 1977, 1981). Recently, it has been shown that *M. affinis* is able to localize conspecific clicks very well (Patrick Stewart, unpublished data). It is plausible that sound production assists them in localizing each other since they exhibit schooling behavior in unclear water.

Future experiments examining the behavioral context of loricariid sounds are needed to see if specific acoustical characteristics are associated with specific behaviors (courtship, aggression, alarm calls, etc.) and to compare the acoustical characteristics of sounds recorded in the wild to those elicited by distress in captivity. Little is known about the effects of the swim bladder on sound production via pectoral spine stridulation. Experiments in which the swim bladders of channel catfish (*Ictalurus punctatus*) were deflated and stridulation sounds were recorded were inconclusive as only two fish vocalized after swim bladder deflation (Fine et al., 1997). Additional experiments are needed in which sounds are recorded before and after swim bladder puncture to see if the swim bladder can modify the frequency or amplitude of the sounds produced by catfish stridulation.

LITERATURE CITED

[1] Bass AH, Clark CW. The physical acoustics of underwater sound communication. In: Simmons AM, Popper AN, Fay RR, editors. Acoustic Communication. New York, NY: Springer-Verlag New York, Inc; 2003 p. 15-64.

[2] Briggs J. The biogeography of otophysan fishes (Ostariophysi: Otophysi): a new appraisal. J Biogeogr 2005;32:287-294.

[3] Connaughton MA, Taylor MH, Fine ML. Effects of fish size and temperature on weakfish disturbance calls: Implications for the mechanism of sound generation. J Exp Biol 2003;203:1503-1512.

[4] Demski LS, Gerald JW, Popper AN. Central and peripheral mechanisms of teleost sound production. Oxford Univ. Press; 1973;13:1141-1167.

[5] Fine ML, McElroy D, Rafi J, King CB, Loesser KE, Newton S. Lateralization of pectoral stridulation sound production in the channel catfish. Physiol Behav 1995;60:753-757.

[6] Fine ML, Friel JP, McElroy D, King CB, Loesser KE, Newton S. Spine locking and sound production in the channel catfish *Ictalurus punctatus*. ASIH 1997;4:777-790.

[7] Fine ML, King CB, Friel, KE, Newton S. Sound production and locking of the pectoral spine of the channel catfish. Amer Fish Soc Symp 1999;24:105-114.

[8] Ganier H. Neuromuscular mechanisms of sound production and pectoral spine locking in the Banjo Catfish, *Bunocephalus Species*. Physiol Zool 1967;40:296-306.

[9] Gohlke, P. (ed.). Aristoteles. Tierkunde. 2nd ed. Ferdinand Schöningh, Paderborn, Germany; 1957.

[10] Hans E, Seidel I. In *Catfish Atlas* Vol 1: South American catfishes of the family Loricariidae, Cetopsidae, Nematogenyidae and Trichomycteridae. Hans A. Bänsch: Melle, Germany; 2005.

[11] Heyd A & Pfeiffer W. Über die Lauterzeugung der Welse (Siluroidei, Ostariophysi, Teleostei) und ihre zusammenhang mit der phylogenese und der schrekreaktion. Rev Suisse Zool 2000;107:165-211.

[12] Kaatz IM. The evolution of sound design in arioid catfish. Amer Zool 1995; 35: 16a, Abstr.

[13] Kaatz IM. The behavioral and morphological diversity of sound communication systems in a clade of tropical catfishes, with comparison to then additional acoustic catfish families (Order Siluriformes, Superfamily Aroidei). PhD dissertation, State Univ. of New York, Syracuse, NY; 1999.

[14] Kaatz IM, Stewart DJ, Rice AN, Lobel PS. Differences in pectoral fin spine morphology between vocal and silent clades of catfishes (Order Siluriformes): Ecomorphological implications. Curr Zool 2010;56:73-89.

[15] Keszka S, Panicz R, Tański A. First record of the leopard pleco, *Pterygoplichthys gibbiceps* (Actinopterygii, Loricariidae) in the Brda River in the centre of Bydgoszcz (Northern Poland). Acta Ichthyol Pisc 2008;38:135-138.

[16] Kner R. Die Hypostomiden. Zweiten hauptgruppe der familie der panzerfische. (Loricata v. Goniodontes). Sitzung der Mathematisch-Naturwissenschatftlichen Classe der Kaiserlichen Akademie der Wissenschaften; 1854.

[17] Ladich F. Comparative analysis of swimbladder (drumming) and pectoral (stridulation) sounds in three families of catfishes. Bioacoustics 1997; 8:185-208.

[18] Ladich F. Acoustic communication and the evolution of hearing in fishes. Phil Trans R Soc Lond 2000;335:1285-1288.

[19] Ladich F, Bass A. Sonic/vocal motor pathways in catfishes: Comparisons with other teolosts. Brain Behav Evol 1998;15:315-330.

[20] Ladich F, Fine ML. Sound-generating mechanisms in fishes: a unique diversity in vertebrates. In: Ladich F, Collin SP, Moller P, Kapoor BG, editors. Communication in Fishes Vol 1. Entfield, NH: Science Publishers, Inc; 2006 p. 3-43.

[21] Ladich F, Fine ML. Sound production, spine locking, and related adaptions. In: Ladich F, Collin SP, Moller P, Kapoor BG, editors. Catfishes, Vol 1. Entfield, NH: Science Publishers, Inc; 2003:249-290.

[22] Markyl. H. Das Schutzverhalten eines Welses (*Hassar orestis* Steindachner) gegen Angriffe von Piranhas (*Serrasalmus nattereri* Kner). Z Tierpsychol 1968;74:39-56.

[23] Myrberg Jr. AA, Ha SJ, Shambott MJ. The sounds of bicolor damselfish (*Pomacentrus partitus*): Predictors of body size and a spectral basis for individual recognition and assessment. J Acoust Soc Am 1993;94:3067-3070.

[24] Parmentier E, Fabri G, Kaatz I, Decloux N, Planes S, Vandewalle P. Functional study of the pectoral spine stridulation mechanism in different mochokid catfishes. J Exp Biol 2010;213:1107-1114.

[25] Pruzsinszky I, Ladich F. Sound production and reproductive behaviour of the armoured catfish *Corydoras paleatus* (Callichthyidae). Environ Biol Fish 1998;53:183-191.

[26] Schachner G. Mechanismen und biologische bedeutung der schallerzeugung und wahrneh-mung beim sudamerikanischen antennenwels (*Pimelodus sp*., Pimelodidae). Unpubl. Ph.D. diss. Univ. of Vienna, Vienna, Austria; 1977.

[27] Schaefer SA. The Neotropical casudinhos: Systematics and biogeography of the *Otocinclus* catfishes (Siluriformes: Loricariidae). Proc Acad Natl Sci Philad 1997;148:1-120.

[28] Tavolga WN. Mechanisms for directional hearing in the sea catfish (*Arius felis*). J Exp Biol 1977;67:97-115.

[29] Tavolga WN. Auditory acuity in the sea catfish (*Arius felis*). J Exp Biol 1981;96:367-376.

[30] Teugels, GG. State of the art recent Siluriform Systematics. In: Ladich F, Collin SP, Moller P, Kapoor BG, editors. Catfishes Vol 1. Entfield, NH: Science Publishers, Inc; 2006 p. 317-352.

[31] Weitzman SH. Hearing in catfishes, especially that of the family Loricariidae. In: Hans-Georg E, Seidel I, editors. Catfish Atlas Vol 1: South American catfishes of the family Loricariidae, Cetopsidae, Nematogenyidae and Trichomycteridae. Hans A. Bänsch: Melle, Germany; 2005.